

SUMMER BIOLOGY OF THE GADWALL AT DELTA, MANITOBA

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IN conjunction with a study of Gadwall (*Anas strepera*) molts carried out at the Delta Waterfowl Research Station in southern Manitoba (1962-64), data on other aspects of summer biology were gathered. In the main, studies on the Gadwall have concentrated on breeding biology with special emphasis on productivity or related factors. The present paper attempts to demonstrate the relationship between breeding and postbreeding activities. Wherever possible, comparisons between wild and hand-reared captive populations have been made.

NESTING

First Gadwalls appeared in mid-April though the peak arrival of residents did not develop until early May of 1964. This peak was 23 days earlier than the average date of nest initiation. Considering that Sowls (1955) and Dane (1966) have shown the length of time between arrival and laying to be dependent upon local weather conditions, the period of 23 days here observed is not strikingly different from the 28 day period recorded by Gates (1962) at Ogden Bay, Utah.

Nest initiation.—The average initiation dates at Delta of nine wild nests in 1963 was 26 May (range 22 May to 1 June), of 21 wild nests in 1964 was 29 May (range 24 May to 6 June), and of nine captive nests in 1964 was 28 May (range 17 May to 11 June). These averages are just a few days later than those recorded at Ogden Bay in 1956-57 (Gates, 1962). At Lower Souris, North Dakota in 1959-60. the average initiation date was about a week later than at Delta (Duebbert, 1966) whereas, judging from hatching peaks, nest initiation at Pea and Bodie Islands, North Carolina was one or two weeks earlier than at Delta (Parnell and Quay, 1965).

Nest sites.—In the wild, nest sites did not differ in any significant way from descriptions already in the literature (Miller and Collins, 1954; Gates, 1962; and others). In general, nests at initiation were surrounded by dense green cover, were on dry ground, and were near water (especially on islands, peninsulas, and dikes). For a detailed description of vegetation, cover, and surrounding landmarks see Oring (1966). In captivity nests were tolerated as close as 2½ meters provided they were initiated 10-15 days apart. Chronological spacing of nests seemingly was brought about by a high intensity of aggression. When the aggression peak of one drake subsided, another pair was able to initiate a nest where previously it had been thwarted. Duebbert (1966) did not observe chronological spacing of nests

in his study of a dense island population. In captivity, a few nests were built in abnormal places such as a plywood box and a reed basket but most sites were typical of those in the wild.

Clutch size and laying.—Eight first clutches in the wild averaged 11.75 in 1963 as compared to 10.05 for 18 initial clutches in 1964. This difference, significant at the five per cent level according to an unpaired *t*-test, is probably due to my having collected most of the hens in the study area in 1963. Most of the 1964 clutches were therefore laid by yearlings. Dane (1965) has shown that yearling Blue-winged Teal (*Anas discors*) lay smaller clutches than do older birds. The combined average of 26 wild nests was 10.57 (range 8–14) compared to 8.67 (range 5–11) for nine nests in captivity. This difference is significant at the one per cent level according to an unpaired *t*-test. The average clutch size of 92 Gadwall nests which Gates (1962) considered initial was 11.1—a figure not significantly different from the combined average of my 26 nests. His assumption that all nests with 10 or more eggs were initial and that all with nine or fewer eggs were re-nests may have raised his average a little. The average size of 686 clutches in northern California (Miller and Collins, 1954; Rienecker and Anderson, 1960) was 11.0 (excluding parasitic eggs). In a dense island population, however, Duebbert (1966) observed an average clutch size of only 9.6 for 130 nests. The smallness of clutches in captivity and in dense island populations may be a result of crowded conditions.

Of 43 nests found in the wild at Delta, four were re-nests and two others may have been. Duebbert (1966) observed a similar low incidence of re-nesting at Lower Souris but Gates (1962) found a significantly greater proportion of re-nests at Ogden Bay. Since success rates at Delta and Ogden Bay were nearly identical, this may best be explained by the fact that some birds at Ogden Bay began nesting as much as two weeks earlier than at Delta and that the summer season in Utah is longer. The birds therefore had more time in which to nest following predation or desertion. Sowls (1955) and Gates (1962) have shown that second Gadwall clutches are smaller than initial ones. At Delta, four re-nests averaged 8.25 (range 6–9). The differences I observed between initial (10.57 average) and re-nest clutch sizes were, according to an unpaired *t*-test, significant at the one per cent level.

In captivity, all eggs were laid before noon. Hens sat on nests four to six hours each day of the laying period. The earliest a hen was known to leave a nest without being disturbed and after having laid an egg was 11:15. No hen spent the night on the nest during the laying period. Duebbert (1966) reported that eggs in the wild were normally laid between 05:00 and 07:00 at Lower Souris.

Incubation period.—Gadwall incubation periods have been stated to be

from 21 or 22 days (Hochbaum, 1944) to 28 days (Witherby et al., 1939). In 1964, 50 eggs in six clutches required an average of 24.0 days incubation (range 22–26) in the hatchery as compared to 25.75 days (range 24–27) for 69 eggs in eight clutches incubated by hens. The difference as determined by an unpaired *t*-test was significant at the one per cent level. Hatchery incubators were kept at 99° F and 90–100 per cent relative humidity. In view of the fact that the total amount of heat above a certain threshold influences the length of the incubation period (Kendeigh, 1963), it is not surprising that such variation in incubation period has been recorded. Dane (1966) has discussed in detail factors affecting the incubation period of the Blue-winged Teal. He found that incubation periods were normally slightly longer in the Delta incubators than they were out-of-doors, but that during extended cold spells, incubation periods outside were considerably lengthened. I did not investigate the influence of weather upon Gadwall incubation.

Hatching, predation, and desertion.—Of 30 wild nests, 14 (46 per cent) produced one or more chicks, 11 (37 per cent) were depredated, and five (17 per cent) were deserted. Other studies have yielded success rates varying from seven per cent (Anderson, 1956) to 92.7 per cent (Duebbert, 1966). Six nests at Delta were apparently depredated by ground squirrels (*Citellus* spp.), four by raccoons (*Procyon lotor*), and one by a striped skunk (*Mephitis mephitis*). It is significant that no instances of avian predation were recorded. Crows (*Corvus brachyrhynchos*) have been exterminated from the Delta area and no gulls (*Larus* spp.) bred nearby.

Two cases of desertion were apparently due to storms, two to human disturbance, and one to predation. A nest containing 11 eggs that I found 8 July 1964 had no eggs the following day. After clearing the area, I found five eggs containing live embryos in three widespread places, all about three meters from the nest. Another nest (9 eggs) located near a construction site was deserted the day I found it. Two nests were deserted in the midst of heavy rains. One held a full clutch, the other two eggs. A nest containing five eggs when I found it, contained a broken egg as well as four intact eggs when I later visited it.

I took the eggs from 3 of 10 captive nests. Another was destroyed by a raccoon. Two of the remaining six were deserted, one on the night of a very severe storm eight days after the start of incubation, the other between the fourth and ninth day of incubation. The remaining four nests hatched a total of 27 young.

Pair bond dissolution.—In captivity, pair bonds were broken at various stages of the breeding cycle. One male left his mate just after she had laid her fifth egg to chase another female whose nest had just been robbed. All other males (7) whose mates incubated eggs, remained with them during

some portion of the incubation period. One drake remained until the 23rd day of incubation—the day before the eggs hatched. All of the males (9) deserted their mates between 12 and 22 June. In a pen where six pairs bred, one pair bond was dissolved on 13 June, four 15 June, and one 18 June. Two of the 15 June dissolutions represented nests from which I took the eggs 11 June, at which time the pair bonds were still intact. One of the two pairs just mentioned joined a postbreeding group together; the female of the second pair was won over by a male with whom she had not previously associated.

Gates (1962), Duebbert (1966), and Oring (1962) observed similar variability in desertion times. Gates (1962) felt that although drakes usually left the hens early in the season, before the middle of incubation, some remained until hatching. This is precisely what I observed in captivity. In my opinion, the sight of postbreeding groups may hasten the breaking of pair bonds. In early June, few such groups—all small—are extant. Later, large aggregations are common.

I watched the dissolution of one pair bond closely. Early in the incubation period whenever the hen was flushed from her nest or left it for a break, she immediately joined her mate. He responded by frequent quacks and Head-bobs. By the 10th day of incubation the drake still accepted the hen and chased nearby males but he no longer quacked and his Head-bobs were infrequent. On the 15th day of incubation the hen, when flushed from the nest, joined her mate immediately, following him down the ditch. She was still aggressive toward foreign birds and chased them but the drake ignored strangers and no longer paid attention to her. On the following day (16th day of incubation) I saw the pair together but the male was not in the least aggressive toward other birds and he neither bobbed nor quacked. By the 19th day of incubation the hen made no attempt to join her mate. The attraction between the two was severed.

POSTBREEDING ACTIVITIES

All captive drakes were still with their mates the first week in June. Pursuit flights were frequent though most males were rapidly molting their body feathers. By 5 June, four of seven drakes in one pen had bred and all were obviously molting. A fifth, which later became the last in the pen to breed, had molted considerably fewer feathers than the four mentioned above. The two remaining drakes in that pen were unsuccessful in their attempts to mate. They had no visible feathers of the basic plumage until 20–22 June.

By the end of June pursuit flights in the wild had ceased: hens were deserted. Molting concentrations which had been increasing for several

weeks were at maximum size. Duebbert (1966) reported a large number of pursuit flights continuing until mid-July at Lower Souris. At Delta during most of July, wild and captive birds spent most of each day sitting along shorelines preening or sleeping. Most feeding was restricted to the early morning and late evening hours. Not until 23 July did I actually observe a flightless Gadwall, but on that date 10–15 per cent of the birds I saw were flightless; many that I saw or collected had just dropped their remiges; and a wild drake that I collected was almost ready to fly again. By 23 July no adults in any of the breeding pens had dropped their remiges. In two large enclosures housing nonbreeding birds, 3 of 14 wing-clipped females and 8 of 10 wing-clipped drakes had dropped their remiges. In other words, 54 per cent of a nonbreeding population had become flightless, a percentage substantially greater than my estimate of the flightless portion of the wild population. By 5 August, about 50 per cent of the wild adult males were flightless but I saw no flightless females. On the same day, 9 of 10 nonbreeding captive males and 6 of 14 nonbreeding captive females were flightless.

Yearling males are apparently less likely to breed than older birds. In pens where all drakes were yearlings there was little breeding and very few pairs formed. Most two-year-old captive males, on the other hand, bred. Of 15 wild males shot while they accompanied their mates in June (14) and July (1), only three were yearlings as determined by the presence of juvenal upper wing coverts. I have collected just three unpaired drakes in June; all were yearlings. Gates (1962) stated that the first Gadwalls to arrive in Utah in spring were unmated yearling drakes. The drake mentioned above which had almost full grown wings 23 July 1964 may have been just such a yearling which never became involved in courtship. In my opinion, there are a few wild Gadwalls, primarily yearling males, that never participate in courtship activities and these few birds, as well as males thwarted very early in their nuptial efforts, are the first to form postbreeding groups and to molt their remiges. They are followed by early breeding males, by later breeding drakes, by nonbreeding drakes which were not thwarted in their sexual efforts until the season was well along, by early breeding hens, and finally by late breeding hens. The discovery in Louisiana of flightless adult females (Chabreck, 1966) leaves opened the possibility that late breeding hens normally migrate before growing new flight feathers.

One of the captive breeding males became flightless during the third week in June due to badly worn feathers. When these feathers became wet, they absorbed water, and the drake was as incapable of flight as he would have been had he dropped his remiges. Several other males in the pen likewise had badly worn primaries and were able to rise from the water only at very



FIG. 1. Seventh Primaries of Gadwalls in Summer Illustrating Variation in Feather Wear.

gradual angles. I have, on three occasions, taken ducks in the wild showing this same condition. One, an adult female Lesser Scaup (*Aythya affinis*), was so obviously flightless on the water that I didn't realize she actually had a full complement of flight feathers until some time after I had shot her. Another hen scaup that I caught by hand was alert and in fine bright plumage but the flight feathers of her right wing were almost devoid of barbs. A flightless male Gadwall that I collected had many broken flight feathers though none had fallen out. Various degrees of wear in primary feathers are shown in Figure 1.

In the breeding pens only 2 of 21 drakes were flightless by 5 August and neither of these had bred. This may have been due to the fact that I pruned the vegetation of these pens in late July—at about the time the birds would normally have dropped their remiges. The disturbance and lack of suitable cover for hiding may have been responsible for failure of the birds to molt at the normal time. Dense concealing vegetation is, I believe, as essential for suitability of a molting area as are water and proper food. In the Delta Marshes, molting areas all contained dense stands of bulrush (*Scirpus* spp.) or cattail (*Typha latifolia*). Freedom of movement may also be essential. In the large pens where adequate vegetation was available and freedom of movement was guaranteed, birds molted normally. Hochbaum (1944) states that the suitability of a marsh as a haven for flightless dabbling ducks depends upon its providing food, cover, and isolation.

The activity schedule of captives in one pen was studied on 7 August when my assistant and I took turns watching continuously from a blind from 04:30 (1½ hours before sunrise) to 22:30 hours (1¼ hours after sunset). A few days later we watched these same birds from 21:00 to 02:00. Only 2 of 13 adults fed during the early morning hours. Starting at 06:30 there was a half hour period of rapid, nervous swimming back and forth. Otherwise the flock preened and slept until 08:15. Feeding picked up markedly during the middle of the day and reached a peak in early evening. At dark, the nervous swimming recurred. The flock swam back and forth, crawled onto land, re-entered the water, and occasionally flew to the opposite side of the pen only to swim rapidly back to the starting point. There was no evidence of feeding between 23:00 and 02:00.

Perhaps the nervousness exhibited by these captives at dawn and dusk was indicative of *Zugunruhe*. These captives still had old remiges but adults in the wild were testing new wings by mid-August. The wild flocks too were restless, moved about a great deal, and fed throughout the middle of the day.

During the remainder of August and in early September, Gadwall flocks increased greatly in size. These flocks were wary, but they fed throughout the day if undisturbed. Their favorite feeding grounds were areas in which fruit-clusters of pondweed (*Potamogeton* spp.) were numerous. By mid-September Gadwalls were leaving the Delta Marshes; by the end of the month they were rare.

GONAD SIZE

Sowls (1955) collected six female Pintails (*Anas acuta*) which were searching for nest-sites and found their largest ova to be 5–7 mm in diameter. Phillips and van Tienhoven (1962) discussed the development of Pintail ova only from the 6 mm stage on (development past the time of first appearance of yellow yolk) since most ovaries contained many ova smaller than 6 mm but only a few that were larger. Both hen Pintails (Phillips and van Tienhoven, 1962) and hen Gadwalls collected prior to nest initiation had an average of six ova larger than 6 mm in the ovary. These species lay an egg a day. In the Gadwall, I found that seven days were required for ova to develop from the 6 mm stage to the 33–37 mm stage at ovulation. Benoit (1950) estimated the period of total ovarian development to be 5–13 days in domestic fowl (*Gallus gallus*), 14 days in domestic Rock Dove (*Columba livia*), and 10–13 days in domestic Mallard (*Anas platyrhynchos*). At ovulation, Gadwall ova measured 33–37 × 31–33 mm. During the three days preceding ovulation, ova measured 21–28 × 15–27 mm; 16–20 × 16–19 mm; and 10–12 × 10–12 mm. Ova were more or less spherical except during the two days prior to ovulation when they assumed a more oblong shape.

TABLE 1
WEIGHTS OF MALE GADWALLS AT VARIOUS STAGES OF BREEDING CYCLE

Stage of annual cycle	Sample size	Extremes (in grams)	Average (in grams)
Paired, 2+ yrs. old	2	866-1,039	952.5
Unpaired, yearlings	2	744- 771	757.5
With laying or incubating females	12	688- 908	822.1
In postbreeding flock before wing molt	2	930- 965	948.5
In midst of dropping remiges	2	874-1,038	956
With 9th primary 1-50 mm	9	869-1,006	914.4
With 9th primary 51-100 mm	8	840-1,004	912.4
With 9th primary 101-122 mm	10	753- 935	839.3

Males arrived on the breeding grounds with somewhat enlarged testes. Three drakes collected while they were chasing unmated hens had testes averaging 26×10.3 mm (left) and 18.3×8 mm (right). Fourteen males attending hens had testes averaging 34.4×16.4 mm (left) and 27.2×13.5 mm (right). In 16 of 17 drakes, the left testis was larger than the right by an average of 6.6×2.4 mm. Two not-yet-flightless adult drakes collected from a postbreeding aggregation each had testes less than 8 mm long. The testes of 27 flightless adult drakes were all between 6 and 15 mm long.

WEIGHT

Although weights of Gadwalls have been included in numerous writings, no one has attempted to correlate weight changes during the summer season with breeding and molting as Weller (1957) did so successfully with the Redhead (*Aythya americana*). In Illinois during the southbound migration adult male Gadwalls averaged 990 grams, juvenile males 908 grams, adult

TABLE 2
WEIGHTS OF FEMALE GADWALLS AT VARIOUS STAGES OF BREEDING CYCLE

Stage of annual cycle	Sample size	Extremes (in grams)	Average (in grams)
Not yet laying (ova less than 38 mm)	4	751- 962	842.75
Laying—full sized egg in duct	3	852-1,031	929.3
With eggs incubated 1-12 days	8	625- 757	682.5
With eggs incubated 13+ days	5	574- 685	631.2
With brood 7 days old or less	5	655- 786	695.6
With brood 8-14 days old	4	730- 803	759.5
With brood 15+ days old	4	695- 789	738.75
Flightless; brood deserted with 9th primary 33 mm long	1		796

TABLE 3
WEIGHTS OF GADWALLS DURING SUMMER MONTHS

Sex	Month	Sample size	Extremes (in grams)	Average (in grams)
♂	May	4	744-1,039	855
♂	June	11	674- 908	821
♂	July	17	831-1,038	937
♂	August	15	753- 931	849
♀	May	1		962
♀	June	14	603-1,031	765
♀	July	18	574- 803	698
♀	August	4	658- 796	731

females 849 grams, and juvenile females 808 grams (Bellrose and Hawkins, 1947). Leopold (1919, 1921) reported that Gadwalls (sex and age classes combined) averaged 850 grams during fall and winter in New Mexico and Texas. Kortright (1942) stated that drakes averaged 908 grams (range 709-1135) and females 823 grams (range 596-1021) but he did not mention what season or seasons his data represented. Nelson and Martin (1953), lumping all data, found 104 males to average 908 grams (maximum 1181) and 89 females to average 817 grams (maximum 1362). Tables 1 and 2 categorize, according to stages of the breeding cycle, 81 wild Gadwalls (47 males, 34 females) taken in southern Manitoba. Drakes gained weight rapidly after deserting their mates. Their weight then remained relatively constant until the final stages of wing-molt at which time they lost about 75 grams. Hens lost a great deal of weight during the incubation period but regained weight rapidly while rearing their broods. Females probably lose a good deal of weight while growing new wing feathers but the loss could not be determined from my data. Table 3 presents weight averages for Gadwalls of both sexes during the summer months. These averages reflect the normal activities of Gadwalls during these months.

SUMMARY

In 1963-64, most Gadwalls initiated nests during the last week of May. Nest-sites were usually in dense cover, on dry ground, and near water. First clutches in the wild averaged 10.57 eggs as compared to 8.67 for initial clutches in captivity and 8.25 for re-nest clutches in the wild. Incubation periods averaged 24.0 days in the hatchery and 25.75 days out-of-doors. In the wild, 46 per cent of 30 nests were successful, 37 per cent were depredated, and 17 per cent were deserted. In captivity, pair bonds were severed at various stages of the breeding cycle but nearly all were broken between 12 and 22 June. In the wild, drakes were with their mates in early June but by the end of the month no pairs were intact.

Nonbreeding drakes that were never active in courtship molted before breeding drakes did, whereas males which did not breed but which attempted to court, molted after breeding drakes. By mid-summer some birds became flightless due to badly worn remiges. Disturbance coupled with lack of cover inhibited wing-molt in captives. Once wild adults regained flight in late summer they were wary and formed large flocks which were soon to depart.

About six days were required for ova to develop from the 6 mm stage to ovulation. Testes of mated drakes were larger than those of unmated drakes that were chasing hens. Testes regressed rapidly once drakes deserted their hens.

Males were heaviest just before dropping their remiges but lost about 100 grams during the flightless period. Females were heaviest during laying, lost weight during the incubation period, and gained weight while rearing broods.

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